

Redescription of the genus and species *Heterovaginina limayana* (Lesson, 1830) (Gastropoda: Soleolifera: Veronicellidae)

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ABSTRACT

Based on the examination of 58 specimens deposited in various institutions, we redescribe the genus *Heterovaginina* Kraus, 1953, considering it monotypic and with its range restricted to Peru. The type species, *H. limayana*, (Lesson, 1830) is also redescribed, and a **neotype designated** for the species. The anatomy of the hermaphroditic region near the female genital pore is emphasized as characteristic of the genus: the copulation bursa is elongated/spheroid, tapering into a distal elongation that folds and joins the bursa duct toward its base, receiving the junctor duct at the tip of the bursa. The rectum penetrates the integument near the female genital pore. There is no penial gland and no accessory gland. The anatomy of the anterior male genital system characterizes the species: smooth penis, with short cylindrical verge that intumescens slightly in its medial region, forming expansions on the sides that mark the beginning of the glans; the penis is longer than the verge, and tapers in its distal portion. There is no spatha. All pertinent bibliography is discussed and the synonymization of *Vaginina odhneri* Hoffmann, 1927, is justified.

INTRODUCTION

The Veronicellidae are terrestrial slugs with worldwide distribution, still poorly known and of uncertain position within the Gastropoda (Hoffmann, 1925; Hyman, 1967; Thomé, 1988a, 1993; Tillier et al., 1996). Among the genera included in the family (Hoffmann, 1925; Forcart, 1953; Thomé, 1975), two share the lack of a penial gland, a structure formed by a papilla and a varied number of tubules, which lies alongside the penis and has systematic importance, although its function is yet not understood.

Of the two genera of the Veronicellidae lacking the penial gland, one occurs in Africa, *Vaginina* Simroth, 1897, and the other, *Heterovaginina*, is restricted to Peru. Simroth characterized *Vaginina* simply by the absence of the penial gland, as opposed to the genus *Va-*

ginula Berthold, 1827 (a synonym of *Vaginulus* Férussac, 1821), which exhibits that structure. In proposing the genus, Simroth (1897) based it on the examination of two specimens without specific names. Only later, that author (Simroth, 1913), examining the same two specimens, described them as *V. conradti* and *V. togoensis*, both originating from the same West African locality. But they differ by the presence of glandular protuberances on one side of the penis sheath in *V. conradti*, and by a smooth sheath in *V. togoensis*.

In his discussion of the nomenclature of the Veronicellidae, Baker (1925) designated *Vaginina conradti* as the type species of *Vaginina*. Hoffmann (1925) accepted *V. conradti* and synonymized *V. togoensis*, maintaining that the character used by Simroth (1913) would be insufficient to differentiate them, in that he had only two specimens, both collected in the same locality. Hoffmann (1925) included the genus in his then new subfamily Meisenheimeriinae, with the following diagnosis, "dark notum, weakly pointed, genital pore almost at mid-length of the hyponotum; with the anterior lobe of the digestive gland behind the anterior loop of the intestine; with the pedal nerves together for a short stretch, parallel and then diverging; with a needle-shaped penis and a basal ringed thickening; without penial gland".

Hoffmann (1927) described *Vaginina odhneri* based on a single specimen of unknown origin, but stating that it was certainly from Africa, despite the fact that *Vaginina*, known only from Africa, was only recorded once. Without discussing the synonyms he had proposed in 1925, he differentiated *V. odhneri* from *V. togoensis* by the shape of the penis, also different from the genus-level morphology he had proposed, and respective sheath and aspects of the copulation bursa and connecting ducts. He adds that in his species the lobe of the digestive gland is in front of the anterior loop of the intestine, also different from the proposed genus-level morphology.

Foreart (1953), in his monograph on African Veronicellidae, considered *Vaginina* as a subgenus of *Pseudoveronicella*, stating that it differs from the other subgenera included in the genus by the characteristics of the copulatory organs and the presence of canals and ducts between the rectum and the ureter, without discussing, at neither the genus nor the subgenus level, the absence or presence of the penial gland. Foreart (1953) agreed with the synonymy of Hoffmann (1925) and considered *Pseudoveronicella (Vaginina) conradti* as a valid name. Without discussion and without examining specimens, he also added *Pseudoveronicella (Vaginina) odhneri* (Hoffmann) to his list as from "probably Africa". He also proposed a new species, *Pseudoveronicella (Vaginina) duporti*, observing that this would differ from the others in the subgenus by the presence of the penial gland (which in fact sets the species apart).

Kraus (1953a) proposed the taxon *Heterovaginina* as a subgenus of *Vaginina*, based on the description of *Vaginina (Heterovaginina) peruviana*, from Lomas de Atocongo, near Lima, Peru, and included *V. odhneri* due to the similarities of the two species. He excluded *V. conradti* because the anterior intestinal loop is anterior to the digestive gland, the copulation bursa has a long duct, and the penis has a much different shape. Kraus (1953b), without any reference to Baker (1925) or to Hoffmann (1925), but mentioning verbal contact with Foreart (Basel, Switzerland) and based on the work of Degner (1934) on the anatomy of *V. togocensis*, raises *Heterovaginina* to the genus level. Kraus stated that, after examining histological sections of a paratype of *H. peruviana*, he found it had a cloaca and lacked the links between the rectum and the fourth ureter, thereby differing from the African genus that, according to Degner (1934), had separate openings for the rectum and the fourth ureter that were connected to each other by a urethral canal and 5 urethral ducts (which were used in the description by Foreart (1953)). Later on, Kraus (1954) synonymized *Heterovaginina peruviana* Kraus, 1953, with *Vaginulus limayanus* Lesson, 1830, considering that, according to personal information from W. Weyrauch, "only one species occurs" in the type locality.

Foreart (1957), after examining Peruvian specimens in the Field Museum of Natural History (now re-examined by us), found them to represent *Vaginina odhneri*, but concluded that this species should be included in the genus *Heterovaginina* because it occurs in southern Peru. He thus agreed with Kraus (1953a), although he did not state so directly.

Thomé (1954) redescribed the holotype of *Vaginina (Heterovaginina) peruviana* Kraus, 1953, deposited in the Senckenberg Museum, Frankfurt-am-Main, without discussing the synonymy. The copulation bursa is, according to Thomé (1954), sac-like and sessile in *V. (H.) peruviana*, which, as we know to be present only in juvenile specimens (Thomé, 1975), in a revision of the American genera of Veronicellidae, recognized and re-described (still only on the basis of the juvenile type specimen) *Heterovaginina* keeping it monotypic (*H. pe-*

ruviana) and with occurrence restricted to Peru. He did not mention *V. odhneri*.

In addition, Thomé (1954) redescribed the holotype of *H. odhneri*, deposited in the Naturhistoriska Riksmuseet of Stockholm, Sweden. According to Thomé (1954), the copulation bursa is spheroid, seated over a thick cylindrical uniform duct and has a short, slender junctor duct that penetrates the copulation bursa duct at mid-length. An inspection of its illustration (Figure 18, p. 44) and knowledge that the material was damaged, lead us to infer that the copulation bursa had actually been pushed down along its duct. Thus, the junctor duct is in part adhering to the bursa duct and does not penetrate it. The junctor duct must, certainly, penetrate the tip of the damaged copulation bursa. The penis is short and broad, with a short, level/convex verge that continues toward the spheroid glans. This latter is transversally widened, with a lateral conical protuberance projecting from the level face of the verge. Thomé et al. (1999) reported a preliminary illustrated redescription of the genus, which is now presented herein in an expanded format.

During the examination of the specimens and of the literature to define the species of the Veronicellidae occurring in Peru, several specimens, both juvenile and adult, were found in the examined collections. These were positively identified as *Heterovaginina limayana* (Lesson, 1830). Based on this material we propose the validity of the genus and the species, with their respective redescrptions and the designation of a neotype.

MATERIALS AND METHODS

Fifty-eight specimens from 26 lots were examined, from the collections of the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MUSM), Lima, Peru; Senckenberg Museum (SMF), Frankfurt-am-Main, Germany; Field Museum of Natural History (FMNH), Chicago, USA; British Museum of Natural History (BMNH), London, England; Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul (MCP-PUCRS), Porto Alegre, RS, Brazil; National Museum of Natural History (USNM), Washington, DC, USA (Thomé et al., 1997) and Naturhistoriska Riksmuseet (NRS), Stockholm, Sweden (Thomé, 1954).

For study of the internal anatomy, the specimens were dissected, starting with a posterior to anterior longitudinal ventral incision, following the methodology of Thomé and Lopes (1973) and subsequent improvements. The mandible (= jaw, of some authors) and radula of two specimens from lots MCP 6594 and MUSM 2513/b were extracted under the stereomicroscope and later analyzed and measured under the scanning electron microscope. The averages of length, width, and distance between the region of greatest width and the anterior tip of twenty rachidian teeth and twenty lateral teeth were calculated. The anatomic, generic and specific,

characteristics are emphasized, following Hoffmann (1925) and Thomé (1975, 1985a, 1985b, 1993).

SYSTEMATICS

Genus *Heterovaginina* Kraus, 1953

Heterovaginina Kraus, 1953a: 63–65.

Type Species: *Vaginina (Heterovaginina) peruviana* Kraus, 1953a: 63–65 (= *Heterovaginina limayana* (Lesson, 1830)).

Diagnosis: The rectum penetrates the integument near the female genital pore. The thin-tissued copulation bursa is spheroid, tapering in a distal lengthening that bends and joins the bursa duct toward its base, receiving the junctor duct at the bursa tip. The bursa duct, of more rigid tissue, is cylindrical and extremely short in the juvenile animal, but lengthens in the adult, becoming an elongated/spheroid bursa. No accessory gland and no penial gland are to be found.

Distribution: Restricted to Peru, South America.

Heterovaginina limayana (Lesson, 1830)

Vaginulus limayanus Lesson, 1830: 302–303, 471, pl. 14, figs. 1–1A.

Vaginula limayana Deshayes in Férussac and Deshayes, 1819: 1851: 96^b–96^c, pl. SE, fig. 14 (exact copy of Lesson, 1830).

Vaginina odhneri Hoffmann, 1927: 26, figs. 11–14; Thomé 1954: 34–36, figs. 14–19.

Pseudoveronicella (Vaginina) odhneri, Forcart, 1953: 60.

Vaginina (Heterovaginina) peruviana Kraus, 1953a: 63–65; Thomé, 1969: 357, figs. 29–30, 45.

Vaginina (Heterovaginina) odhneri: Kraus, 1953a: 63–65.

Heterovaginina limayana: Kraus, 1954: 52–53.

Heterovaginina odhneri: Forcart, 1957: 96.

Diagnosis: Penis smooth, short cylindrical verge that intunnescens a little beyond the middle of its length, forming expansions on the sides that mark the beginning of the glans. Glans longer than the verge, tapering in its distal portion; generally curved. There is no spatula.

Redescription: *External Anatomy.* A large portion of the examined material is externally very discolored. However, the color pattern on the notum showed the following general characteristics: specimens with light chestnut colored notum with irregularly distributed black dots and splotches, nevertheless clearly showing two longitudinal black lines that delimit a lozenge-shaped mid-region. Between these two lines a fine light streak occurs centrally in the notum, starting apart from the anterior perinotum at about ¼ of the way down the full length of the animal and continuing to the rear without reaching the posterior perinotum. (Averages of the external dimensions, in 20 specimens (measurements in mm): notum length = 29.20, width = 13.90, height = 7.14; width of the sole = 4.41; width of the right hypostomum = 4.14, distance from the female genital pore forward = 11.50, and behind = 12.90; distance from the female genital pore to the pedal furrow = 0.73.)

Internal Anatomy. Salivary gland well developed, formed by large and prominent acini, some quite loose, others compact. Anterior intestinal loop, covered by the anterior lobe of the digestive gland.

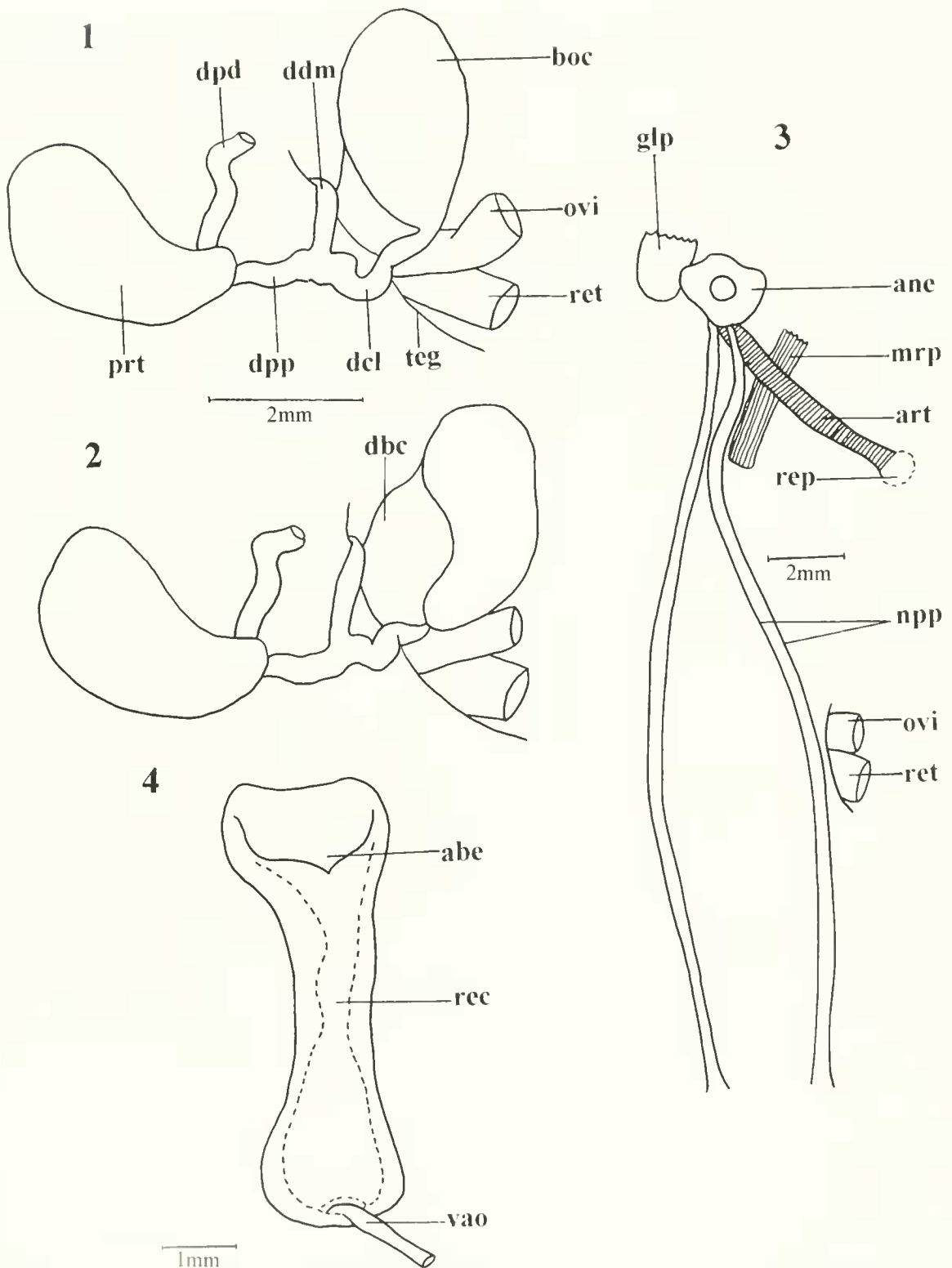
The two nerve pairs, pedal and palial, originate very close to the respective ganglia of the perisophageal ring and stretch through the central cavity in two sets, right and left, which separate from each other about a fourth of the way from their starting place, continuing thus almost to the end of the central body cavity, where they come slightly closer and penetrate the integument (Figure 3). The anterior aortic artery meets the nerves near their beginning (in anterior direction) (Figure 3). The posterior pedal branch of the aortic artery was not found. (Average measurements of the nerves in 20 specimens in mm: total length = 29.9; together = 418; apart = 16.5; maximum separation = 2.72 mm; meeting of the aortic artery = 1.76 mm from the origin.)

Pedal gland (Figure 4) short, flattened, broad in its proximal portion, narrowing in the middle with the posterior extremity rounded and somewhat broadened, dorsal opening scalloped; longitudinally three areas are visible, a translucent outer one on each side, and a slightly rough central one that is higher, narrower, and yellowish. At the distal extremity of this central area is the penetration scar of the inferior branch of the aortic artery, right under the nerve ganglia. (Average dimension of the pedal gland in 20 specimens (in mm): length in the natural position = 1.20; distended (dorsal surface) = 1.11; greatest width = 1.90.)

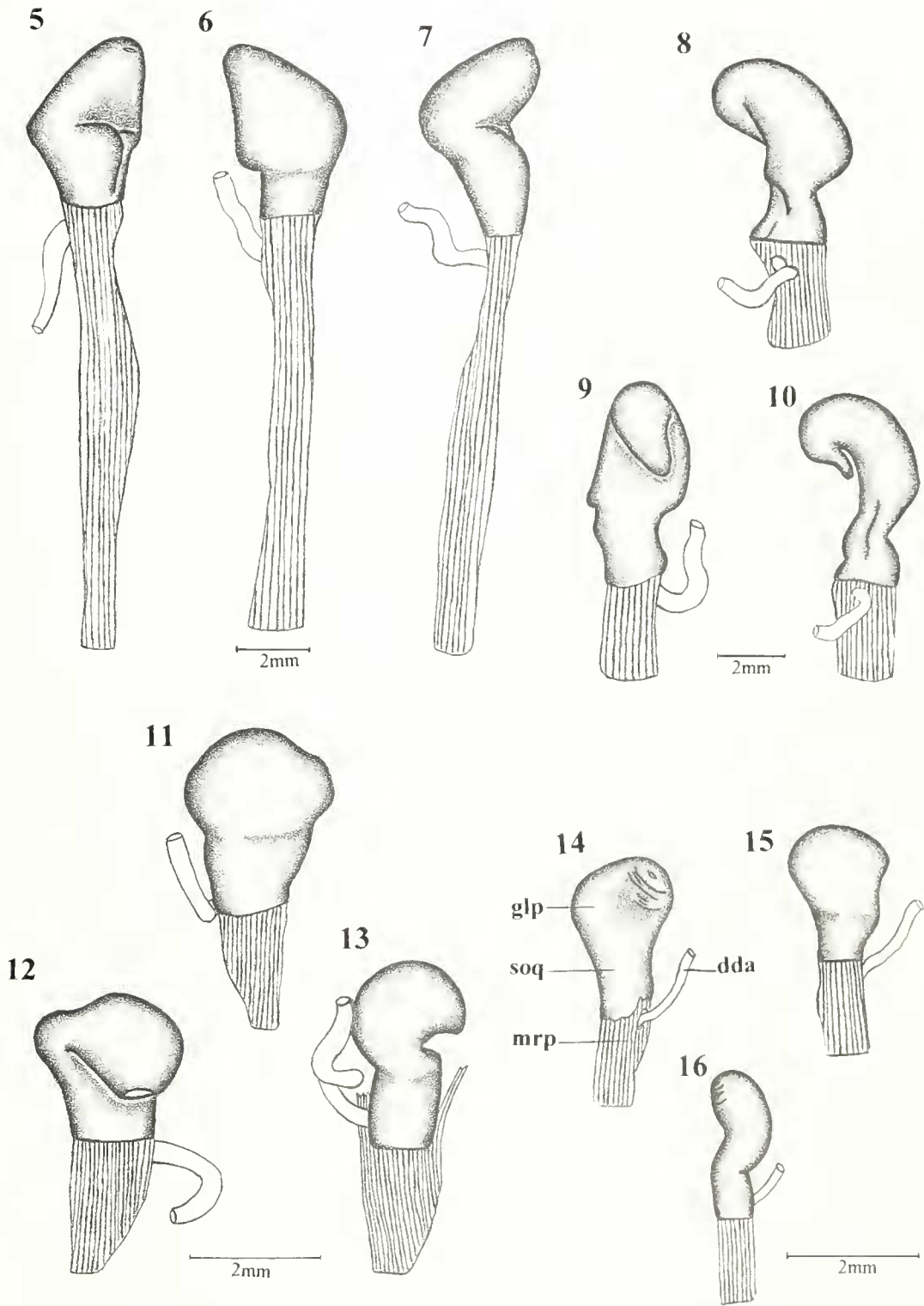
The thin-tissued copulation bursa (= spermatheca or spermatolytic gland, of some authors) is spheroid, tapering in a distal lengthening that folds and joins the bursa duct toward its base, receiving the junctor duct (= canalis junctor of some authors) at the bursa tip. The bursa duct, of more rigid tissue, is cylindrical and extremely short in the juvenile animal, but lengthens in the adult, becoming an elongated/spheroid bursa. The junctor duct is thick and sinuous, narrowing slightly in its final portion, when, after entwining part of the base of the bursa duct, it penetrates into the narrowest part of the copulation bursa itself. The rectum penetrates the integument near the female genital pore (Figures 1, 2). No accessory gland (= accessory bursa of some authors) was found.

Penis smooth, with a short, cylindrical verge, swelling a bit beyond the middle of its full length, forming on the sides two expansions that mark the beginning of the glans. Glans longer than the verge, becoming slender in its distal portion; generally curved. Retractor muscle of the penis very variable in length (Figures 5–16). There is no spatula. (Average dimensions of the penis in 20 specimens (in mm): total length = 2.26; greatest diameter of the glans = 1.15; verge length = 1.02; verge diameter = 1.07.

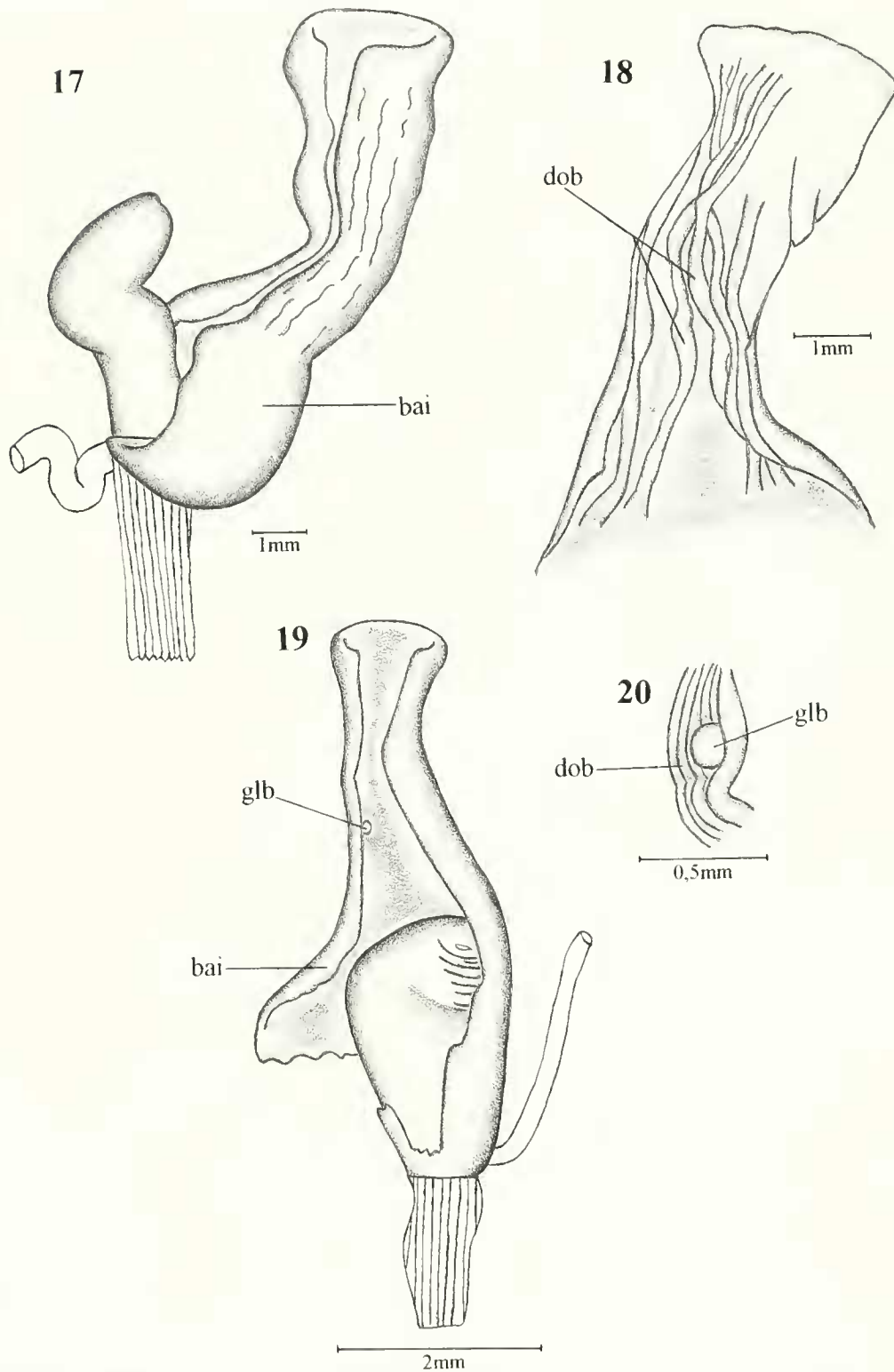
The sheath surrounding the penis (Figure 17) has two distinct regions, clearly differentiated by the well-defined presence of two different types of tissue. The proximal portion of the sheath, which surrounds the penis



Figures 1-4. *Nautilus limayana*. 1, 2. Part of the posterior genital organs and of the rectum (MCP 6594). 3. Arrangement of the pedal nerves (MCP 6594). 4. Pedal gland (MCP 6594). abc: opening; anc: nerve ring; art: anterior aortic artery; boc: copulation bursa; dbc: copulation bursa duct; dcl: ejaculator duct; ddm: middle deferens; dpd: distal posterior deferens; dpp: proximal posterior deferens; glp: part of the pedal gland; mrp: retractor muscle of the penis; npp: pair of pedal and palial nerves; ovi: part of the oviduct; prt: prostate; rec: central region; rep: pericardial region; ret: part of the rectum; teg: integument; vao: part of the inferior branch of the aortic artery.



Figures 5–16. *Heteroagalina limayana*. 5–13. Three different views of the penis, in 3 adult specimens, respectively MUSM 2513/b (Figures 5–7), MUSM 1455 (Figures 8–10), FMNH 59456/a. Figures 11–13. 14–16. Three different views of the penis in one juvenile specimen (FMNH 59456/b), dda: anterior portion of the deferens duct, glp: glans; mrp: retractor muscle of the penis; soq: verge.



Figures 17-20. *Nautilus limayana*. 17. Sheath that envelops the penis, opened longitudinally (MUSM 2513/b). 18. View of the distal portion of the penis sheath, showing the sharp longitudinal folds of the internal tissue (MUSM 2513/b). 19. Sheath, opened longitudinally, showing the presence of a salient globular formation of the internal tissue, similar to that described by Hoffmann (1927) for *Nautilus* as a gland (FMNH 59486/b). 20. Region of the salient globular formation, greatly enlarged, also showing details of the internal folds (FMNH 59486/b). bai: sheath; dob: folds; glb: salient globular formation.

is extremely thin, often allowing visualization of the penis by transparency. The distal portion, starting from a significant constriction right after the tip of the penis, which is swollen, has numerous longitudinal folds internally and a porous and yellowish (glandular?) aspect. These folds may be more or less tight, neatly arranged, and rectilinear (especially in juvenile specimens) or in disarray (Figure 18). Even in juvenile specimens where the male region is little developed, the miniscule folds (Figure 20) can be seen inside the sheath. The penial gland is absent.

The mandible is formed by an average of 23 lathis (= ribs, of some authors), very visible and somewhat separated one from the other. The most central lathis are a bit taller than the others. No transverse grooves were noted, perhaps due to the obvious wear. The average length and greatest width of the mandible, in the same lots utilized for extraction of the radulae, were 2.1 mm and 0.5 mm respectively (Figure 21).

The radula has a great number of lateral teeth, distributed rectilinearly in columns parallel to the single, central line of rachidian teeth, which are always smaller. An average of 103 columns and 120 transverse rows were counted, resulting in a calculation of 12360 teeth per radula. The average dimensions of the radula were 5.55 mm length by 3.41 mm at the greatest width. The average dimensions of 20 lateral teeth were: length 56.2 μ m, width 24.5 μ m, distances from the greatest width to the tip 29.43 μ m. The average dimensions of 20 rachidian teeth were: length 32.5 μ m, width 12.5 μ m, distance from the greatest width to the tip 17.0 μ m. (Figures 22–23).

Neotype (herein designated): MUSM 4001, from type locality, 24 Jan. 2002, leg. Rina Ramírez and Ulises Zamora.

Type Locality: Peru, Dpto. Lima, Cerro San Cristobal, (12°01'45.1" N, 77°00'52.6" W), 215 m above sea level.

Other Material Examined: MUSM 4001, (neotype), Peru, Dpto. Lima, Cerro San Cristobal (12°01'45.1" N, 77°00'52.6" W), 215 m above sea level, 24 Jan. 2002, leg. Rina Ramírez and Ulises Zamora; MUSM 1000, 2 specimens, same data as the neotype; MUSM 1458, 1 specimen, Peru, Dpto. Lima, Bosque Zárate (11°54' N, 76°29' W), 3000 m above sea level, 24 Mar. 1978, leg. Valencia and Franke; MUSM 1460a, 1 specimen, Peru, Dpto. Lima, Bosque Zárate (11°54' N, 76°29' W) (Chourritos II), 2850 m above sea level, 01 Mar. 1980, leg. Valencia and Franke; MUSM 1660, 4 specimens, Peru, Dpto. Lima, Lomas de Atocongo (Steinloma) (12°13' N, 76°54' W), 28 Sep. 1951, leg. Koepecke (Kp340m); MUSM 1807a, 3 specimens, Peru, Dpto. Lima, Surco (11°52' N, 76°28' W), leg. Koepecke (Kp1010a); MUSM 2388, 1 specimen, Peru, Dpto. Lima, Surco (11°52' N, 76°28' W), 2100 m above sea level, 17 Aug. 1965; MUSM 2389, 1 specimen, Peru, Dpto. Lima, Distrito de San Borja, (Rio Surco), (12°06'

N, 77°01' W), 08 Jun. 1986, leg. A. Rossi, MUSM 2513, 3 specimens, Peru, Lima, Huachipa (12°00' N, 76°56' W); MUSM 3251, 2 specimens, Peru, Dpto. Lima, Canta (Cullhuay) (11°19' N, 76°33' W), 3550 m above sea level, 24 Mar. 1989, leg. H. Sisniegas; SMF 108548, holotype of *Vaginina Heterovaginina peruviana*, Peru, Dpto. Lima, Lomas de Atocongo (12°13' N, 76°54' W), 28 Oct. 1951, leg. Koepecke; SMF 323293.1, 1 specimen (ex-MUSM 4000), same data as holotype; SMF 140062/7, 7 specimens, Peru, Dpto. Lima, Cerro San Cristobal, leg. W. Weyrauch; FMNH 59486, 8 specimens, Peru, Dpto. Lima, April 1948, leg. W. Weyrauch; FMNH 59487, 6 specimens, Peru, Dpto. Lima, Lomas de Atocongo (12°13' N, 76°54' W), leg. W. Weyrauch; FMNH 59488, 3 specimens, Peru, Oconeque, Puno, 4 Oct. 1941, leg. C. C. Sanborn; FMNH 300744, 1 specimen (ex-MUSM 4000), same data of the neotype; BMNH 20020126, 1 specimen (ex-MUSM 4000), same data of the neotype; MCP 6501, 1 specimen, Peru, Dpto. Lima, Bosque Zárate, (11°54' N, 76°29' W), 3000 m above sea level, 24 Mar. 1978, leg. Valencia and Franke; MCP 6502, 3 specimens, Peru, Dpto. Lima, Surco (11°52' N, 76°28' W), 2100 m above sea level, 17 Aug. 1965; MCP 6504, 1 specimen, Peru, Dpto. Lima, Canta (Cullhuay) (11°19' N, 76°33' W), 3550 m above sea level, 24 Mar. 1989, leg. H. Sisniegas; MCP 6593, 1 specimen, Peru, Lima, Huachipa (12°00' N, 76°56' W); MCP 6594, 1 specimen, Peru, Dpto. Lima, Apr. 1948, leg. W. Weyrauch; MCP 7988, 2 specimens (ex-MUSM 4000), same data of the neotype; USNM 571911, 1 specimen, Peru, NRS 949 1052, holotype of *Vaginina odhneri*.

DISCUSSION

Vaginulus limayanus was briefly described by Lesson (1830), who used a few morphological features in his description. Lesson also offered a color plate, probably prepared in Peru, including dorsal and ventral views of the animal. This specimen was not deposited at the Paris Museum, and could not be found, despite our efforts, in any other major European Museum. It is very likely that Bérard lost the specimen after the artwork was completed. We conclude that there was never a holotype. The description and figures were used by Deshayes (1830–1832) in Ferrussac and Deshayes, with no further comments.

Although the holotype *Vaginina Heterovaginina peruviana* Kraus, 1953, is an immature specimen, the synonymization of this latter species by Kraus (1954) based on information from W. Weyrauch is confirmed after its examination.

Recent collections and observations of live specimens made by our collaborator Rina Ramírez confirm that there is only one species at the type locality and its vicinities.

Therefore, we herein propose the designation of a neotype for the species (see above), deposited at the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MUSM), Lima, Peru, MUSM 4001, and

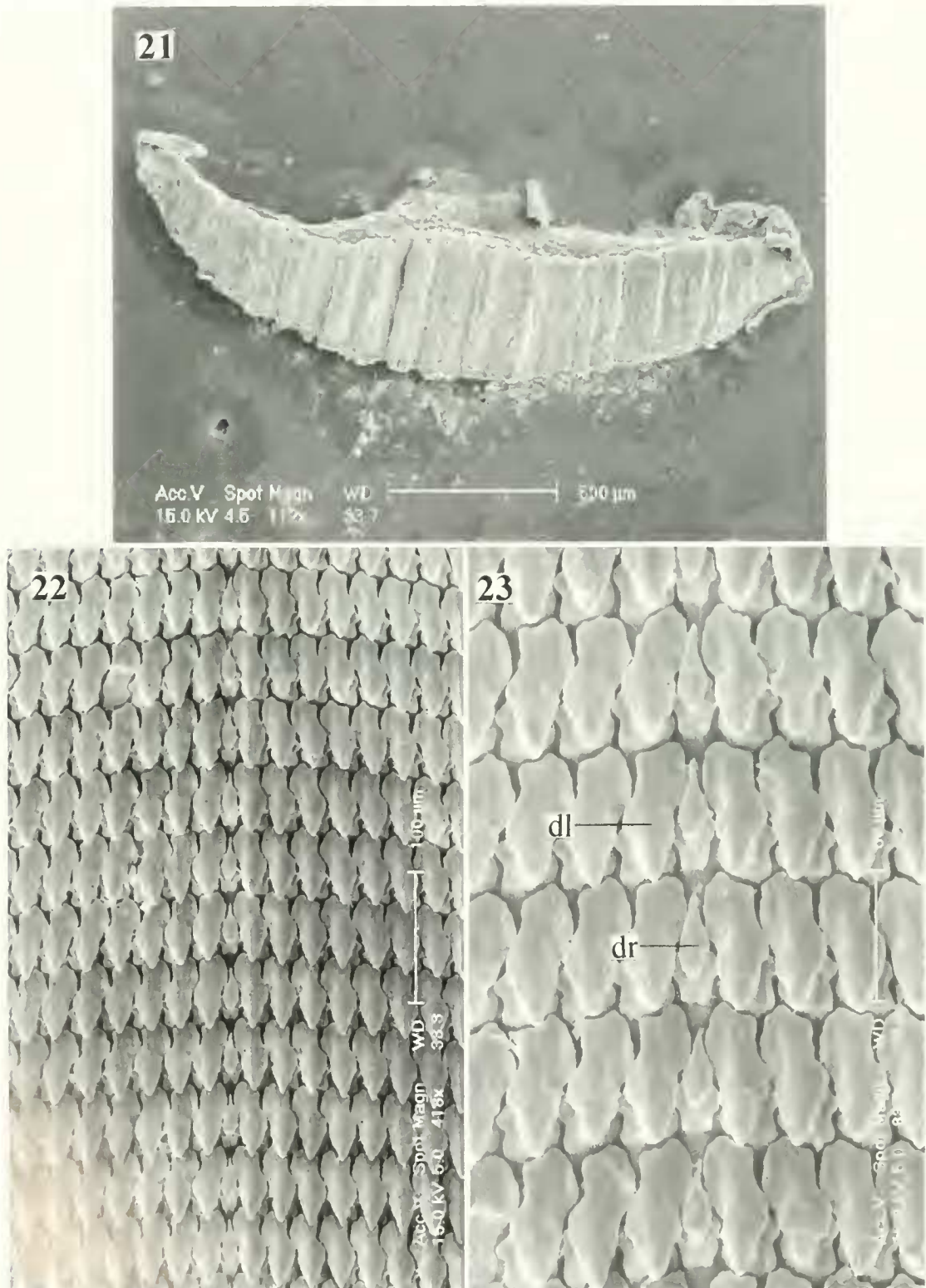


Figure 21. *Nautilus naumanni*. General view of a mandible (MCP 2513/b).
Figures 22-23. *Nautilus naumanni*: Middle region of the rachula. 22, slightly and 23, greatly enlarged (MCP 2513/b). dl: lateral tooth; dr: rachial tooth (central).

collected at the original type locality of the species, Cerro San Cristobal.

Hoffmann (1927) proposed the species *Vaginula odhneri*, especially due to the presence in the penis sheath of a glandular protuberance. Thomé (1954) in his redescription of the holotype of *V. odhneri*, made no reference to that distinctive protuberance because the holotype was extensively damaged.

In three juvenile specimens (SMF 10554S, MCP 6593, and FMHN 59486/d), among them the holotype of *H. peruviana* (= *H. limayana*), an almost circular protuberance on the inner wall of the penis sheath was found, very similar to that described by Hoffmann (1927) for *H. odhneri* as a "gland". The "gland" described for *H. odhneri*, used to distinguish it from *H. limayana* ("sensu" Kraus), appears to be only a more salient, globular formation of the internal tissue of the sheath, because its texture is the same as this tissue (not a "gland") (Figures 19–20).

Despite the additions and changes made herein, the dichotomous key for determining the American genera, proposed by Thomé (1975), continues to be valid for *Heterovaginina*.

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